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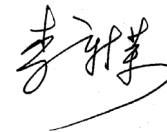
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Ecological adaptation of common reed and eco-hydrological significance of biological soil crusts in arid regions of China

Desert ecosystems commonly have a sparse vegetation cover and are characterized by a distinct patchiness comprised of vascular plants and biological soil crusts (BSCs), consisting cryptogam due to extreme environmental stress. It is important to explore the ecological adaptation of these vascular plants such as common reeds (*Phragmites communis* Trin.) and understand the ecological significance of BSCs for desert ecosystem management. Experimental results indicated that three reed ecotypes (dune reed: DR; Gobi salt reed: GSR and swamp reed: SR) had different adapting responses in foliar surface and mesophyll characteristics. Compared to SR, the two terrestrial ecotypes, DR and GSR, had lower stomatal densities and smaller caliber of stomata. The stomata caved in the leaf surface and a number of crystals like hairs accumulated in the epidermis in DR and GSR, especially in GSR. A particular structure similar to salt gland was found in GSR. In addition to differences in the surface, the two terrestrial ecotypes also exhibited mesophyll differences compared

to SR. Chloroplasts in mesophyll cells were attached to the cell wall and exhibited a long shuttle shape in the two terrestrial ecotypes and an ellipsoid shape chloroplast in SR. Higher density of starch grain exhibited in GSR.

For BSCs, the field experimental results demonstrated that higher soil pH and higher total potassium content in topsoil positively correlated with the colonization of cyanobacteria and algae, while increasing dust deposition onto the topsoil enhanced the development of lichen and mosses in BSCs. Increasing soil moisture raised the proportion of mosses and lichen in BSCs. BSCs changed the spatiotemporal pattern of soil moisture and re-allocation by decreasing rainfall infiltration, increasing topsoil water-holding capacity and altering evaporation. Development of BSCs facilitates arthropod establishment on dunes surface. Various disturbances on crusts may result in decreased a reduction of species richness and abundance of both plants and soil animals in desert systems.



1. Ecological adaptation of common reed

Structural characteristics of the leaf epidermis and chloroplast were investigated in common reed (*Phragmites communis* Trin.) inhabiting in three different habitats in the Tengger Desert, northwest China: dune reed (DR); Gobi salt reed (GSR) and swamp reed (SR). Leaf epidermis, mesophyll cells and chloroplasts were detected by scanning electron microscopy and transmission electron microscopy, respectively. The results indicated that foliar surface and mesophyll had different adapting responses for different ecotypes of reeds. Compared to SR, the two terrestrial ecotypes, DR and GSR, had lower stomatal densities and smaller caliber of stomata. The stomata caved in the leaf surface and a number of crystals like hairs accumulated in the epidermis in DR and GSR, especially in GSR. A particular structure similar to salt gland was found in GSR. In addition to differences in the surface, the two terrestrial ecotypes also exhibited mesophyll differences compared to SR. Chloroplasts in mesophyll cells were attached to the cell wall and exhibited a long shuttle shape in the two terrestrial ecotypes and an ellipsoid shape chloroplast in SR. Higher density of starch grain exhibited in GSR. These results suggest that

the adaptation of common reed to saline or drought-prone dunes triggers changes in the organs related to apperceive environmental conditions could contribute to the high resistance of reeds to extreme habitats.

2. Eco-hydrological significance of BSCs

BSCs are one of the major components of desert ecosystems, which vary from 2 mm thick, relatively homogeneous cyanobacteria crusts (Zaady et al., 1997; Zaady and Bouskila, 2002), to complex crusts dominated by lichens and mosses that are up to 30 mm thick on the surface of stabilized sand dunes (Li et al., 2002). We studied their roles in arid desert systems on the following three aspects:

1) The relationship between BSCs and Microgeomorphology features

We tested the hypothesis that micro-geomorphological features determine the spatial distribution of BSCs by reallocating related abiotic resources at small- and medium-scales in the Tengger Desert. In order to determine the micro-geomorphological influences on BSC distribution, small soil mounds (diameter <2 m) with xerophytic shrubs and herb cover on the southern slope (slope angle 5°–15°) of the massif of Xiangshan Moun-

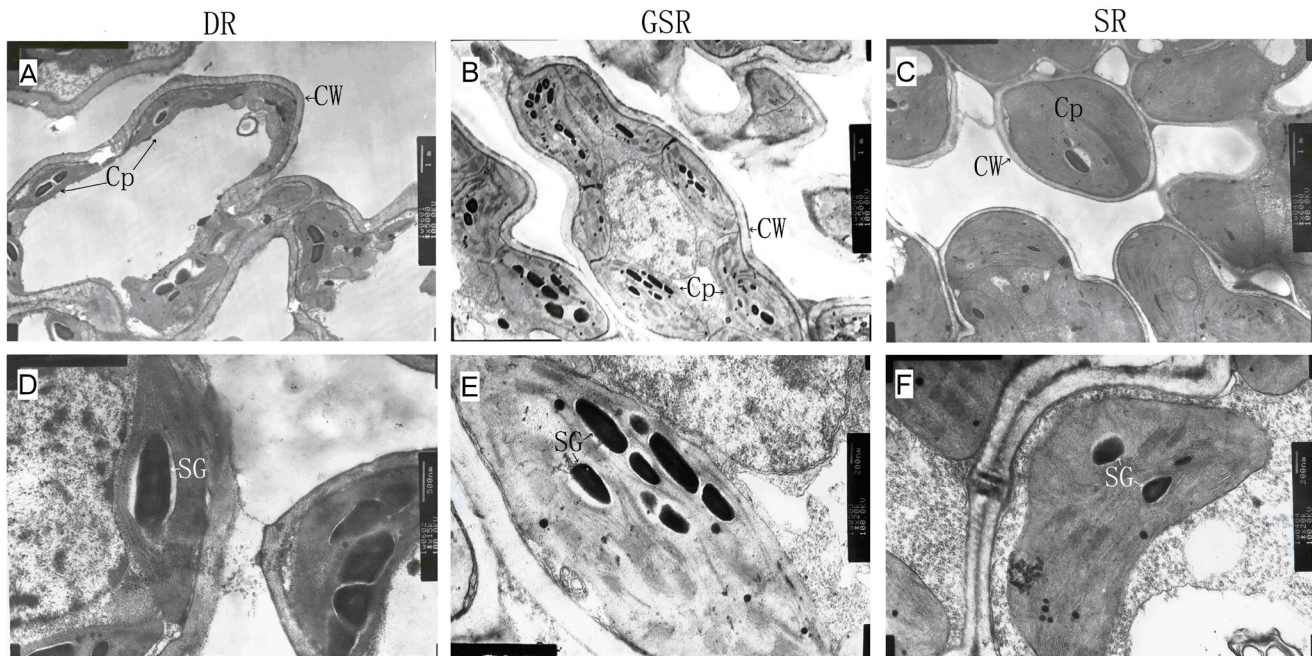


Fig 1. Transmission electron microscopy of mesophyll cells and chloroplasts of reed leaves in three ecotypes (A, B and C, mesophyll cells; D, E and F, chloroplast. CW, cell wall; Cp, chloroplast; SG, starch grain)

tain, southern Tengger Desert were chosen as Site 1 for sampling and surveying cryptogam communities. In comparison with Site 1, 10 plots located on the crest, windward slope, leeward slope and the hollow of dunes stabilized by revegetation (Site 2) were investigated and sampled to distinguish the effects of soil properties on BSCs and scale effects of micro-geomorphological influences. Site 2 differs from Site 1 in soil texture, soil thickness and nutrients (Li et al., 2005; Li et al., 2008).

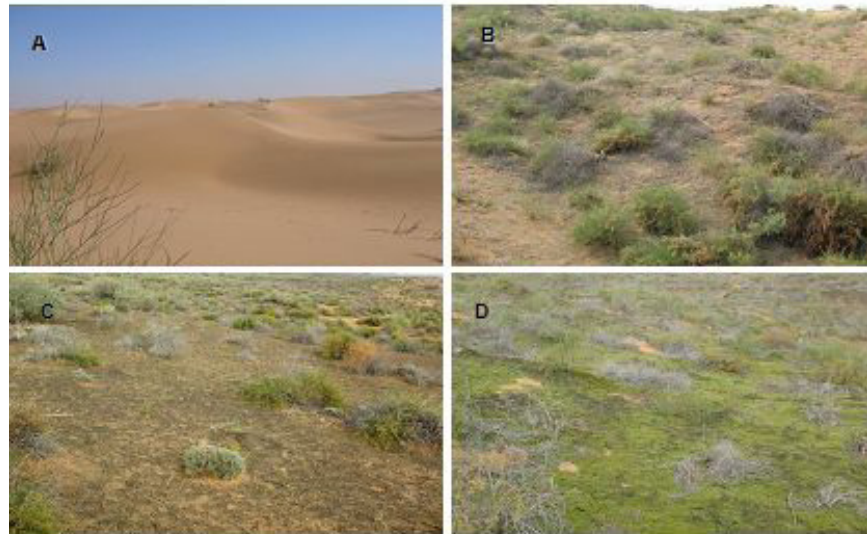
Our results showed that higher soil pH and higher total potassium content in topsoil positively correlated with the colonization of cyanobacteria and algae in the earliest successional stages of BSCs, while increasing dust deposition onto the topsoil enhanced the development of lichen and mosses in the later stages of BSCs. Increasing soil moisture raised the proportion of mosses and lichen in BSCs, this will possibly change the ecological functions of BSCs, such as nitrogen-fixation by cyanobacteria, due to the conversion from a complex to relative simple type of BSC. Micro-geomorphology has created various habitats at a small-scale affecting colonization and development of cryptogams. This paper considers the contribution of micro-geomor-

phology to biodiversity in the extreme arid desert systems.

2) Hydrological effects of BSCs on sand-binding vegetation

It is difficult to identify the hydrological effects of BSCs in desert systems, and the results of recently conducted studies on their effects are debatable (Belnap, 2006). Moreover, few studies have been devoted to the link between artificial vegetation dynamics and BSCs in stabilized dunes. We conducted this study to determine if the occurrence and development of BSCs in the Tengger Desert could be used to determine sand-binding vegetation changes via altering soil moisture and water cycling using long-term monitoring data and field experimental observation. The study sites are located at the southeast fringe of the Tengger Desert in the Shapotou region of the Ningxia Hui Autonomous Region, western China. The mean annual precipitation is 186 mm, approximately 80% of which falls between May and September. The annual potential evaporation is 2800 mm. The landscape of the Shapotou region is characterized by large and dense reticulate barchan chains of sand dunes. To understand the actual effects of BSCs on the water cyc-

les in the revegetated areas of sand dunes, we directly measured the infiltration depth after different rainfall events at four sites: dunes stabilized using the same revegetation method in 1956, 1964 and 1982 and a control site (mobile dune). These different-aged sites support different types of crusts. Specifically, cyanobacteria and algae crusts are dominant in areas that were revegetated in 1982 (site 1), while lichen crusts dominate areas that were revegetated in 1964 (site 2) and mosses dominate areas that were revegetated in 1956 (site 3, Figure 2). The maximum soil water-holding capacity, evaporation, dew entrapment were determined, in addition, long-term changes in soil moisture at the three different-aged sites were evaluated using the long term monitoring data provided by the Shapotou Desert Research and Experiment Station, Chinese Ecological Research Network (CERN), CAS. Our results indicate the presence of BSCs, especially moss and lichen crust, led to a remarkable reduction in infiltration when compared with the control. Specifically, the reduction in infiltration in response to BSCs occurred in the following order: moss crust > lichen crust > algae crust. The topsoil water contents were highly correlated with the infiltration depths. The presence of BSCs obvi-



ously promoted topsoil water content when the one-off rainfall exceeded 5 mm, especially when the topsoil was covered by moss crust. The topsoil water-holding capacity of different BSCs was found to increase in the following order: mobile dune < cyanobacteria and algae crust < lichen crust < moss crust. The presence of BSCs reduced evaporation of topsoil after small rainfall events (2 and 5 mm) when compared with the dune surface, and the lowest evaporation occurred in moss crusted topsoil, while there was no significant difference between algae and

Fig. 2 Sand dunes landscape before establishing sand-binding vegetation (control site, A), sand-binding vegetation with BSC dominated by cyanobacteria and algae, revegetated in 1982 (site 1, B), sand-binding vegetation with BSC dominated by lichens, revegetated in 1964 (site 2, C), sand-binding vegetation with BSC dominated by mosses, revegetated in 1956 (site 3, D)

lichen crusted topsoil. Shallow and deeper soil water contents were primarily characterized by the local rainfall regime during the early period of revegetation, corresponding to the water use of planted shrubs with deeper root systems. As a result, little rain water infiltrated deeper layers of the soil, rainfall influenced weakly on deeper soil water content from 40 to 50 years following revegetation. However, after 50 years of sand-binding vegetation development, the soil water, including deeper soil water content, begun to highly respond to the local rainfall regime. BSCs altered the initial soil water balance of revegetated areas of sand dunes by influencing rainwater infiltration, soil evaporation and dew water entrapment. BSCs improved the soil water availability of the shallow layer by enhancing the topsoil water-holding capacity, which occurred due to increased silt and clay and decreased surface evaporation via absorption by cryptogams. Furthermore, BSCs reduced the amount of rainfall water that reached deeper soil, which is where the roots of shrubs are primarily distributed. Indeed, at least 80% of the annual rainfall was intercepted by BSCs and prevented from infiltration to deeper soil in afforested sand areas. The changes in soil water patterns and topsoil features induced

by BSCs resulted in vegetation replacement or degradation of the initial sand-binding vegetation. As a result, the initial planted shrub-dominated communities were replaced by shallow-rooted herbaceous plants. An extensive, diverse and well-developed BSC would contribute to the colonization of herbaceous plants, while favoring annual over woody species. It is vital to determine a lower and suitable cover of deeper-rooted woody species to ensure the sustainable development of afforested sand-binding vegetation in future large-scale revegetation projects in sandy deserts.

3) Association of ant nests with successional stages of BSCs

With the exception of ecosystem effects on soil physical and chemical properties, hydrological processes and vascular plants, the role of BSCs in shaping the abundance and diversity of desert primary consumers such as ectothermic arthropods has been mostly ignored. In deserts, ants constitute a very important group in terms of abundance, and tend to have specific habitat requirements that are largely determined by microhabitats for thermoregulation, accessibility of predator-free space, and food resource availability.

ty. In this study, we describe these unusual relationships between ant nests and BSCs of different successional stages to determine if BSCs serve as key providers of refuges for soil fauna and insects such as ants in the temperate desert. Specifically, this study was conducted to answer the following questions: (1) Are there any ant species significantly associated with BSCs? (2) Are there differences in the numbers of ant nests on sites covered by different successional crusts? (3) What are the main factors governing these indirect or direct linkages in desert ecosystems? We measured topsoil properties and crustal features during different successional stages, which were characterized by cyanobacteria and algae, lichens, and mosses, respectively. The species richness of ants in sandy desert environments was largely dependent on the presence and development of BSCs due to their creating differences in soil properties and food sources. Ant species distribution varied considerably between the four sampling sites (including the control), where crustal community structures differed (differences in cryptogamic species composition, biomass and coverage), suggesting that the variations in BSCs of different successional stages influence the suitability of the site for

different ants. For example, *F. imitans* and *F. glauca* prefer moss dominated crusts to cyanobacteria and algal crusts during the early stages. This could be also related to the stress tolerance of some ant species. The results of CCA and stepwise regression weighted the biomass and thickness of BSCs and topsoil as key factors influencing the variance in ant nest distribution. The later crusts (mosses and lichens) benefit higher ant species richness and species abundance (represented by the total nest density per plot), indicating that these factors may be soil-related. During the succession of BSCs after sand dunes were stabilized by revegetation, the sandy soil physical and chemical properties were considerably altered by BSCs via increasing silt and clay content as a result of enhanced entrapment of dustfall and surface roughness (Reynolds et al., 2001, Breckle et al., 2008; Li et al., 2010), enhanced soil stability against wind and water erosion due to the formation of aggregative structure by the filaments, rhizoids, thallus and polysaccharides of crustal organisms cementing the soil particles (West, 1990; Eldridge and Greene, 1994). This has resulted in increased input of limited resources to desert ecosystems such as nitrogen and carbon fixation (Evans and

Lange, 2001; Housman et al., 2006; Langhans et al., 2009), as well as changing soil moisture regimes via influences on infiltration, evaporation and water-holding capacity (Li et al., 2002; Wang et al., 2007; Belnap, 2006) and soil temperature by increasing the cover and changing surface color (Belnap and Lange, 2001). These alterations, in turn, facilitate the development of BSCs on dune surfaces (Breckle et al., 2008). Biomass, coverage and the thickness of BSCs and topsoil were obviously higher in the late successional stage than in the early stage, which can be attributed to increases in the proportion of mosses in crustal communities (Shepherd et al., 2002; Li et al., 2010) and accumulation of dustfall deposition by moss entrapment (moss has a higher ability to capture dustfall deposition than other cryptogamic species, Li et al., 2002). The correlation of ant species and nest distribution with biomass, coverage and thickness of BSCs is likely due to the diversity of the microhabitat offered by crusts with different biomass, coverage and thickness, including creating different microclimatic conditions via altering the moisture, temperature and UV-B radiation (Castenholz and Garcia-Pichel, 2000) that reaches the surface. In particular, the higher biomass

and coverage of BSCs may reduce the extreme summer soil temperature, providing a thermo-regulated shelter. Moreover, the relatively thicker crust and topsoil favors nest establishment and protect nests from sand sinking and sand burial (Chen et al., 2007). Thus, the colonization and development of BSCs on the dune surface at least provided a suitable habitat for ant survival. On the other hand, as an important factor ants also contribute to improving soil reducing soil losses and increasing organic matter, as well as enhancing infiltration (Bestelmeyer and Schooley, 1999; Cerda and Jurgensen, 2008; Cerda et al., 2009; Cerda and Doerr, 2010). Our experimental results showed that the removing BSCs from the sandy soil surface (control site) would result in the total loss of these refuges for ants. These findings indicate that the presence and development of BSCs maintain and enhance ant species diversity in desert ecosystems, while various disturbances result in the loss of ant diversity. However, the distribution of ants may modify nest soils by increasing the soil nutrient content and altering the soil structure (Cerda and Jurgensen, 2008), which, in turn, changes the crust cover and biomass (Ayal, 2007; Whitford et al., 2008). The contribution of BSCs to

ant species richness and abundance may also be attributed to their vital food-web function in extreme sandy systems. BSCs provide habitat and refuge to ants from predators, as well as a food source (Belnap, 2001; Li et al., 2008). This results in ants becoming abundant in habitats with high crust biomass and coverage (Li et al., 2006). A more diverse crustal community would presumably support a more diverse range of invertebrates, while ants are the main predators in these microbiotas (Sanchez-Pinero and Gomez, 1995). Similarly, ants also directly feed on some crustal organisms such as lichens and mosses.

Hence, we can conclude that mosses and lichen-dominated crusts, which occur during the late successional stages of BSCs, supported higher species richness and abundance of ants when compared with BSCs in the early successional stages, which were characterized by pioneer cyanobacteria and algal species. The distribution of ant nests was closely associated with most of the measured soil physical and chemical parameters of topsoil covered by BSCs in the different successional stages. Among the soil properties and BSC features, biomass and thickness of BSCs and topsoil were the main factors

governing the distribution of ant nests. In sandy desert ecosystems, the presence and development of BSCs on the dune surface facilitated ant establishment and maintained species diversity, which could be attributed to the creation of suitable habitats and refuge and their providing a vital food source. Various disturbances on BSCs may result in decreased ant diversity in arid desert regions.

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